BEHAVIOR SYSTEMS AND REINFORCEMENT: AN INTEGRATIVE APPROACH

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Most traditional conceptions of reinforcement are based on a simple causal model in which responding is strengthened by the presentation of a reinforcer. I argue that reinforcement is better viewed as the outcome of constraint of a functioning causal system comprised of multiple interrelated causal sequences, complex linkages between causes and effects, and a set of initial conditions. Using a simplified system conception of the reinforcement situation, I review the similarities and drawbacks of traditional reinforcement models and analyze the recent contributions of cognitive, regulatory, and ecological approaches. Finally, I show how the concept of behavior systems can begin to incorporate both traditional and recent conceptions of reinforcement in an integrative approach.

Key words: reinforcement, behavior systems, regulation, cognition, ecology, simple causal models, causal systems, pigeons, rats

Reinforcement has long been a centerpiece of experimental psychology, a concept of marked interest to other disciplines ranging from social work to field biology. Historically, reinforcement can be viewed as the offspring of British associationism and an American functionalist empiricism. British associationists provided an armchair analysis of the determinants of associations among mental events. American experimentalists linked this analysis to manipulable stimuli and readily measurable responses. In American hands, the study of reinforcement focused on the development of a simple causal model of how past consequences of a response alter its future expression. Despite rapid initial progress, pinning down the characteristics of this simple causal relation has proved a daunting task, one that first fractionated and then, during the last few decades, slipped from favor. In this paper I consider why the task of analyzing reinforcement has proved to be so difficult and suggest an integrative approach that begins with the assumption that learning is organized and effectively studied within evolved functional systems of behavior. This approach combines traditional phenomena of response selection and

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association with elements of cognitive, regulatory, and ecological conceptions of learning.

SIMPLE CAUSAL MODELS VERSUS CAUSAL SYSTEMS

When two events occur in spatial and sequential proximity, it is intuitive to conclude that the first event causes the second, particularly if the events are physically linked (e.g., Michotte, 1946). Thus, when one billiard ball strikes another and the latter moves, the first ball is readily presumed to cause the movement of the second. I will refer to such a combination of sequence, proximity, and linkage as a simple causal model. Such simple causal sequences are exceptionally powerful models of the world, because they generate reliable predictions of cause and effect, allow the mapping of functional relations between events, and encourage incorporation of these relations into laws and theories.

Given the same two events as above, again occurring in spatial and sequential proximity, it is much less intuitive to assume that the second event causes changes in the subsequent occurrence of the first event. In the case of two billiard balls, this is akin to assuming that the impact on and movement of the second ball alter the subsequent occurrence of the first ball. This is a causal hypothesis that demands a much more complex explanatory linkage. As fortune would have it, though, this less intuitive form of causality appears to be the type of phenomenon that occurs in reinforcement. The initial event, a response, is followed closely

in time by a second event, presentation and ingestion of a reinforcer, yet the focus is not on the relation of the response to the presentation and ingestion of the reinforcer but on how aspects of the reinforcing event alter the future expression of the initial response.

Because of the separation of the presumed cause and effect, it is not surprising that the phenomenon of reinforcement caused an initial stir on the grounds that it seemed to require back-action of the reinforcer in affecting the response preceding it. How else could the present path of a billiard ball affect the future path of the ball that struck it? Thorndike (1898) was among the first experimentalists to provide a simple link between the second event, the reinforcer, and future responding. He used the concept of stored associations to form a simple causal model relating the reinforcing event to the response. Specifically, Thorndike argued that the reinforcing event strengthened neuronal connections relating the environment and the response. Because of these strengthened connections, the next time a similar situation occurred, the response was more likely to occur.

Though most behaviorists followed Thorndike's lead in filling in a simple causal link between reinforcer and response, Skinner (1981) took a somewhat different tack. He argued that reinforcement was not an example of simple cause and effect but a form of selection by consequences, a causal mode unique to and characteristic of living systems. Eschewing connections between stimuli and responses mediated by neurons, Skinner initially bridged the gap between reinforcer and response with the concept of a reflex reserve built up by previous reinforcements (Skinner, 1938). Later, he linked the reinforcer to the response by means of the concept of the organism's reinforcement history, a history defined in terms of response strengthening mediated by relations between discriminative stimuli and reinforcer availability.

Despite the apparent uniqueness of his conception of how reinforcers relate to responses, at a pragmatic, procedural level Skinner effectively behaved like other behaviorists—as though there were a simple causal relation between the reinforcing event and changes in responding. This simple causal view can be seen in Skinner's accounts of how he shaped responses as well as in his claim (Skinner,

1953, p. 92) that responding "is constructed by a continual process of differential reinforcement from undifferentiated behavior, just as the sculptor shapes his figure from a lump of clay." Learning researchers of most theoretical persuasions almost universally have assumed and supported a simple causal view of reinforcement by carefully documenting reliable functional relations between characteristics of the presentation of the reinforcer and subsequent changes in responding. For example, manipulation of both the frequency and amount of reward produces systematic changes in subsequent responding (Catania & Reynolds, 1968; Kimble, 1961).

Although there is ample evidence of the success of the simple causal model of reinforcement in establishing control of behavior, there is also increasing evidence that it represents a local minimum, interfering with rather than facilitating further development. The adequacy of the simple causal model is questioned by difficulties in predicting results related to issues of stimulus processing and memory (e.g., Gallistel, 1990; Roitblat, 1987) and by the relevance of ecology to phenomena such as misbehavior, superstition, and constraints on learning (Breland & Breland, 1966; Timberlake & Lucas, 1989). There is even surprising difficulty in specifying the necessary and sufficient conditions for reinforcement (Timberlake & Allison, 1974; Timberlake & Farmer-Dougan, 1991). Quite tellingly, many researchers concerned with topics such as learning in ontogeny, cognitive and motor functioning, and the development of social attitudes and norms no longer even mention the concept of reinforcement, replacing it with more complex models involving memory types, categorization mechanisms, and adaptation.

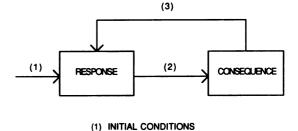
In short, the simple causal model of reinforcement appears to be an oversimplified causal structure imposed on a complex and dynamic biological phenomenon. To begin to deal with the complexity of reinforcement phenomena, it is necessary to combine multiple interrelated causal sequences and reasonable initial conditions within a causal system (e.g., see related parts of Baum, 1973; Powers, 1973; Ray & Delprato, 1989; Staddon, 1980). Figure 1 represents a simple schematic of such a system involving only two events, a response and a consequence. The diagram designates the causal relation between the response and con-

sequence as (2), the relation between the consequence and the occurrence of the response as (3), and the initial conditions and operating characteristics as (1). Excitatory stimulus conditions were intentionally omitted in this simplified representation to focus more attention on the basic structure of the system, but they would be included within all three causal relations. Stimulus conditions affect and are affected by the initial conditions of the system, the response-consequence sequence, and the consequence-response sequence. Within this system, causal sequences like (2) and (3) can be investigated, but it must be recalled that they are not independent causal chains. The output of a functioning system must satisfy all sequences at the same time. Thus, the result of the manipulation of a causal system is the product of the interaction of all causal sequences, not the result of manipulating an isolated determinant of one of them.

Interactive causal systems are relatively common in science, but they require careful specification of how the system operates (see Ray & Delprato, 1989). Changing the simple causal model of reinforcement into a systems approach will require work in at least three areas: clearer linkage between the consequence and the response, consideration of additional causal sequences and their interactions, and specification of initial conditions and operating characteristics of the system.

With respect to the causal relation between the consequence and the response, the size of the typical temporal gap between these events makes it vital to specify the nature of the processes linking them. Skinner's (1966) solution of conceptualizing reinforcement as a new kind of causal mode ultimately cannot take the place of more complete analyses of the causal pathway between a consequence and a response. We cannot wait for brain science to fill this gap (cf. Skinner, 1989). Neuroscience has increasing information to provide but needs considerable help in fitting it together with the analysis of a functioning organism.

Nor is the argument that intervening mediational concepts have been misused a sufficiently compelling reason to shun them. I suspect it is not possible to have a useful scientific model that avoids the use of mediational concepts in any form. The assumption of a simple causal relation between consequence and response is itself a mediational concept that has



(2) RESPONSE CONSEQUENCE RELATION (CONTINGENCY)
(3) CONSEQUENCE-RESPONSE RELATION (REINFORCEMENT)

Fig. 1. A simplified system view of reinforcement: (1) initial conditions, (2) response-consequence relation (contingency), and (3) consequence-response relation (reinforcement).

proved inadequate in several respects and requires clarification if it continues to be used. Our only defense against the misleading aspects of mediational concepts is care in specifying close ties to behavior, ruthless testing of their predictions, and intermittent evaluations of their adequacy and necessity. The present paper is in part an analysis of the necessity and adequacy of the mediational simple causal model of reinforcement.

The second area of change requires consideration of potential causal relations in addition to that between the consequence and the response leading to it (including the relation between environmental stimuli and the response). For example, few experiments have considered the relation between rate or latency of lever pressing and subsequent rate of ingestion or the relation between the rate or quality of drink opportunities and the latency and pattern of drinking, much less how such relations might affect the return relation between the consequence and responding. One reason that other causal relations have been ignored is that the simple causal model of reinforcement (as well as Skinner's notion of selection by consequences) presumes a single critical event, the presentation of a reinforcing consequence. As noted before, from a systems view this is not a simple causal manipulation. Presentation of a reinforcer is an act of the experimenter that constrains the entire functioning system, generating multiple causal sequences and typically producing multiple ef-

One acknowledgment of the complexity of

the reinforcement situation has come with the concept of a feedback function relating the response and the consequence. Though often viewed as an independent variable manipulated by the experimenter, researchers have increasingly viewed a feedback function at least partly as a dependent variable. As pointed out by Baum (1973) and Nevin and Baum (1980), the obtained relation between reinforcer rate and response rate frequently differs from the relation specified by the experimenter. But even this acknowledgment does not go far enough. The subject often modifies the imposed relation in surprisingly complex ways (e.g., Gannon, Smith, & Tierney, 1983), and instrumental responding may have a causal role (see Collier, 1983). For example, the efficiency of pigeons in feeding from a hopper is a complex function of the hopper time assigned by the schedule function rather than, say, a constant proportion of that time (Rashotte & Henderson, 1988; Timberlake & Peden, unpublished data).

Sometimes the initial conditions of a system may interact with a contingency to produce a relation between events where none was imposed by the experimenter. Timberlake and Lucas (1989) reported that under a Pavlovian schedule that programmed a random relation between presentations of rolling ball bearings and food, rats actually held on to the bearings long enough to produce a strong sequential and temporal relation between mouthing the bearings and eating food. To reiterate, the presentation of a reinforcer or the specification of a feedback function is not a simple causal manipulation but a manipulation that alters the functioning of a system, thereby creating potential causal relations and results that are not predictable from experimenter-designated feedback functions. The system essentially "settles" at an output that satisfies all causal sequences at once.

The third change necessary to develop a causal system approach to reinforcement is to specify the initial conditions (the current functioning) of the system prior to the presentation of a reinforcing event. Knowledge of initial conditions is particularly important because they provide the beginning points and operating characteristics that influence the outcome of the causal processes evoked by presenting a reinforcer. Like most traditional learning theorists, Thorndike and Skinner tended to view

the conditions preceding reinforcement as consisting of undifferentiated and even random responding (Timberlake, 1983b). This view has become untenable with the accumulation of examples of the importance of initial conditions (e.g., Breland & Breland, 1966; Brown & Jenkins, 1968; Timberlake & Lucas, 1989). In fact, Gardner and Gardner (1988) argued that initial conditions in the form of feed-forward processes were the most powerful and unappreciated determinant of learned behavior. Although he did not make them an integral part of his basic model of reinforcement, Skinner (1966) also argued for the importance of "phylogenetic" contributions to learning.

In summary, the simple causal model of reinforcement is both too powerful and too impoverished. Though undeniably useful in specific instances and in the short run, the simple causal model is at best an incomplete strategy and at worst a misleading guide to the long-term understanding and prediction of reinforcement. Both its power and impoverishment stem from the same source, a paradigm in which experimenter-defined consequences (reinforcers) are treated as isolated, simple causes of responding. The excessive power of this paradigm lies in the presumption that an experimenter can manipulate responding by means of contingencies with little regard for other situational and organismic variables. The impoverishment comes because not enough is known about the functional systems we constrain with imposed consequences to pinpoint determinants or precisely predict results except in familiar and restricted circumstances.

In the long run, both basic science and practical applications will profit most from a continuing analysis of the contributions of the multiple causal sequences and initial conditions of a causal system to the phenomenon of reinforcement. In the next section I review the traditional associationist/behaviorist approach to reinforcement using the simple systems framework outlined in Figure 1. I then consider three recent conceptual approaches that address issues necessary to develop further a causal system view of reinforcement: cognition (amplifying the simple causal sequence between consequence and responding), regulation (introducing other causal sequences), and ecology (setting the initial conditions). In the final section I suggest the possibility that some of the strengths of the traditional reinforcement approach and recent work on these conceptual approaches can be combined within a behavior systems framework to produce a more complex and integrative approach to reinforcement.

THE CLASSIC ASSOCIATIONIST/ BEHAVIORIST APPROACH

As noted above, the majority of research on reinforcement was given its shape by the translation of British associationism and utilitarianism into the framework of an American pragmatic empiricism. A critical midwife to this transition appears to have been German experimentalism, with medical physiology hovering in the background (including Pavlov, 1927). The present section paints with a broad brush the basic concepts that characterized the view of the British associationists and the American behaviorists. The mode of presentation is based generally on the concepts illustrated in Figure 1 with more explicit consideration of environmental stimuli. This exposition is largely pictorial, with concepts represented as boxes and their relations as connecting arrows. It is motivated by the limited purpose of clarifying concepts and general analytic schemas within the reinforcement approach rather than trying to provide historical completeness or nuance. Thus, there is a lack of acknowledgment of important differences among the views of individuals and little explicit coverage of the continued evolution of particular approaches.

The British Associationists

The British associationists, largely on the basis of introspection, proposed a number of important variables as determinants of the association of mental events (e.g., contiguity, similarity, contrast). Figure 2 shows the critical concepts as memory, an integrator (consciousness of the relation between stimuli), and environmental stimuli. In this view, events enter consciousness from the environment or as representations from memory. Based on characteristics such as proximity in space and time, these events are connected and the association stored in memory.

Although this approach was referenced almost entirely to mental events, there was some attention to initial motivational and constitutional conditions (Warren, 1921), and Spencer

BRITISH ASSOCIATIONISTS

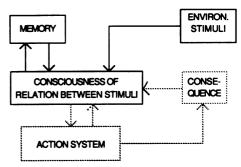


Fig. 2. In an associationist model of learning, environmental stimuli enter consciousness and are related to each other or to stimuli from memory. If the stimuli are sufficiently similar or unique, the result is an association between them. As indicated by the dotted arrows and boxes, some associationists included an action system relating associations to behavior and to consequences such as pleasure or pain.

and Bain brought associations closer to behavior with the hypothesis that the development of sensory motor associations was dependent on pleasurable or painful outcomes. These contributions are represented as the action system and consequence in Figure 2. However, in all cases the basic approach was to work backwards (introspectively) from an existing association to infer its basis, rather than working forward (experimentally) to establish the actual course of its development. None of the important concepts (similarity, contrast, pleasure, or pain) were experimentally realized variables.

Behaviorists and Neobehaviorists

Taking more than a few pages from Lloyd Morgan (1896) and combining them with the rigor of the German experimentalists, American researchers soon provided standard experimental paradigms that anchored learning in the effects on responding of external variables under experimental control. Experimenters manipulated the response-consequence relation (or the conditioned stimulusconsequence relation) and observed the effects on the consequence-response relation. For example, Thorndike's law of effect stated that those responses followed closely by (experimenter controlled) satisfaction will be more firmly connected to the situation so that when it occurs again, they will be more likely to recur. With the partial exception of Skinner,

BEHAVIORISTS & NEOBEHAVIORISTS

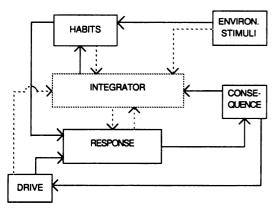


Fig. 3. The solid arrows and boxes (habits, environmental stimuli, response, and drive) show the early behaviorist view that learning consists of the acquisition of single stimulus-response relations (habits) caused by an appropriate response consequence (a reinforcer) in the presence of particular stimuli, with drive modifying the output. The dotted arrows and boxes reflect the neobehaviorist inclusion of additional stimulus sources, including physiological states (drive) and response-produced stimuli.

subsequent behaviorist theorists followed the broad outlines of Thorndike's approach while attempting to tie the notion of satisfaction more firmly to environmental variables. The most prevalent addition was the inclusion of an explicit deprivation condition (drive), the reduction of which triggered learning.

As seen in Figure 3, consciousness was dropped from the model in favor of a more automatic increase in the strength of habits (connections between stimuli and responses) as a function of response consequences called reinforcers. The solid arrows represent the viewpoint of the earlier behaviorists, who attributed learned behavior to the expression of response habits triggered by environmental stimuli. Habits were (neuronal) connections relating the environment and responses that were strengthened by reinforcing consequences. Later behaviorists (represented by the dotted boxes and arrows in Figure 3) depended increasingly on more complex integration of environmental and internal stimuli, habits, drives, and momentary cumulative responding to account for learning.

There were two marked difficulties with the neobehaviorist approach. First, neobehavior-

ists could not settle on the form in which learning was processed, stored, and retrieved. For example, were the connections stimulus-stimulus (S-S), stimulus-response (S-R), or anticipatory-goal-response-anticipatory-goalstimulus $(r_g - s_g)$? Second, they could not come to a satisfactory statement of the relations among drives, reinforcement effects, and characteristics of the consequence, such as amount, frequency, and intermittence. It was not that the neobehaviorist approach did not work; rather, one realization worked better in some circumstances while another worked better in other circumstances. To create a more encompassing theory, it became necessary to add more intervening variables and to attempt to specify their relations.

Eventually, behaviorist theories had either a great weight of conceptual mechanisms tied to a relatively small number of measured variables (e.g., Hull, 1952) or a large number of potential independent variables with only a little conceptual and empirical constraint on their relations (e.g., Tolman's, 1932, equation: behavior = f[stimuli, past training, heredity,and momentary physiological states]). Also, it became increasingly difficult to distinguish among different theories. The nomenclature was different, but the predictions and functions were the same. For example, predictions based on expectancies versus anticipatory goal stimuli and responses could not readily be distinguished (MacCorquodale & Meehl, 1954). Further, apparently important differences in theoretical statements could not be resolved by experiments. For example, whether drive multiplied or added to incentive in determining responding could not be determined without making strong assumptions about the measurement scales involved (Krantz, 1972).

Skinner

Compared to the theoretical disarray and top-heaviness of neobehaviorism, Skinner's reflex-influenced approach was both simple and attractive. As shown in Figure 4, he used a small number of low-level concepts, namely, responses, discriminative stimuli, and reinforcers (consequences)—the three-term contingency. Skinner tried to avoid positing unnecessary mediating variables even as minimal as stimulus—response (S–R) connections. He believed such notions were too closely allied

with the myriad mentalistic concepts that down through history had been unsuccessfully and misleadingly invoked as causes of behavior.

To remove mentalistic concepts, Skinner reduced processing and integration to a single consequence-response relation (including discriminative stimuli) that was strengthened by reinforcers. Initially, Skinner (1938) added the concept of reflex reserve to account for longterm effects of reinforcement (Killeen, 1988; Timberlake, 1988). However, the function of the reflex reserve was gradually taken over by the organism's reinforcement history, a concept that apparently escapes mediational status by residing at the interface of the environment and the subject. The additional concept of drive was used to account for variability in responding and serve as a setting condition or modifier of the reinforcing effects of a consequence on responding (the dotted line in Figure 4; see Michael, 1985; Skinner, 1938).

Skinner's approach followed the behaviorist tradition in its marked externalization of event relations and focus on manipulation of the response-consequence relation as an independent variable. Skinner deviated from the associationist tradition by classifying responseconsequence relations primarily as types of schedule tied to patterns of operant responding, rather than in terms of the traditional associative variables of contiguity and frequency and their effect on response latency in discrete associative trials. He did, though, explicitly emphasize the traditional variables of frequency and contiguity in describing the process of shaping successive approximations to a particular response, and in his analysis of schedule effects as a function of the reinforcement of interresponse times (Michael, 1985). The result was a combination of two approaches to learned behavior: a simple causal model of response shaping based on the traditional associative variables of frequency and contiguity of response and consequence, and a more molar level of analysis concerned with the control of steady-state responding based on the empirically derived effects of imposing work schedules relating responding and payoff.

The conceptual simplicity and pragmatic control possibilities of Skinner's technology encouraged many examples of basic and applied research that related experimenter manipulations of the response-consequence relation to

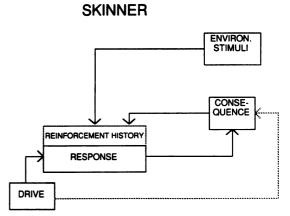


Fig. 4. Skinner's reinforcement model resembles the early behaviorist model in that learning is based on the strengthening of responses in the presence of environmental (discriminative) stimuli as a function of response-contingent consequences (reinforcers). An important difference is that many of the functions subserved by "habit" in the behaviorist model are carried by "reinforcement history" in Skinner's approach. Drive serves as a modifier of responding and (less frequently) as a setting condition and modifier of consequences.

subsequent changes in response rate. Along with its experimental and applied success, though, came the problem of how to develop this conceptual approach further. The neobehaviorist view suffered from an inability to secure agreement on the theoretical concepts connecting consequences and responding. In contrast, Skinner's view suffered from an inability to escape conceptual agreement, either to expand, eliminate, or even test his basic concepts.

A key to both the conceptual simplicity and relative inflexibility of Skinner's approach was his technique of codefining his basic set of concepts—discriminative stimuli, responses, reinforcers (consequences), and reinforcement effect (Jenkins, 1979; Timberlake, 1988). In Skinner's approach, a reinforcer is an event that changes the rate of a response (an operant class) upon which it is closely contingent, a response is a member of a class of movement that is changed in rate by a reinforcer, a stimulus is an environmental change that controls the rate of a response, and reinforcement is a change in response rate that occurs following the presentation of a reinforcer. These phenomena do not exist independently of each other except perhaps in the form of "candidates," a term Skinner disliked but that appropriately implies that reinforcers, responses, and stimuli have been selected in a preliminary way by the experimenter but cannot be actually confirmed until reinforcement occurs (Timberlake, 1988).

I believe it is no accident that the primary conceptual advances in traditional operant psychology have focused on relative choice (the relative distribution of responding across alternative consequences) in restricted conditions (Fantino & Abarca, 1985; Herrnstein, 1970). Most operant choice experiments have dealt with the relation of rates of similar reinforcers to rates of similar responses on similar schedules. These circumstances require dealing only with relative measures of frequency and rate. The use of different responses and reward types soon requires the specification and analysis of potential mediational variables, such as the concept of "reinforcing value."

In short, Skinner's approach combined a pragmatic simple causal model of reinforcement for shaping responses with a conceptual definition of reinforcement that is associated with empirical openness to experimenter manipulations but is not readily falsified or developed. This package has been readily ported to different fields, resulting in many advances in the control of behavior in new circumstances and organisms. But although study of the relations between consequences and responses can add to the base of empirical knowledge, it cannot affect Skinner's conceptual analysis.

In summary, American behaviorists translated associations between events in consciousness into relations between external consequences and responses. They replaced the philosopher's technique of working backwards from observed associations to inferred causal variables by the experimental technique of manipulating the relation between the response and the consequence and examining the effects on future responding. Despite this agreement on general approach, researchers were not able to agree on consequence-response rules, the number of roles played by environmental stimuli, the basis for remembering, or even how best to manipulate response-consequence rules (e.g., continuous schedules vs. single trials). In addition, with the exception of motivation, the importance of initial conditions in affecting responding received little systematic attention. Generality of prediction was achieved by different strategies: markedly increasing the number of intervening variables, simplifying the presumed causal sequence, or codefining concepts only as they produced a reinforcement effect.

MORE RECENT APPROACHES TO REINFORCEMENT

Although there is no question about the power of the reinforcement approach developed by American behaviorists, new concerns have emerged. In this section, I review three recent approaches to the study of reinforcement—cognitive, regulatory, and ecological that deal primarily with phenomena and variables that have been deemphasized or omitted in traditional research. The cognitive approach instituted a more careful consideration of stages of stimulus processing and the learning and remembering of multiple stimuli and their relations. The regulatory (motivational) approach clarified determinants of total responding and the necessary and sufficient conditions of reinforcement. The ecological approach provided conceptions of and information about the initial conditions and operating characteristics that constitute the organismic context of reinforcement. Because these approaches tend to amplify one aspect of the causal system used in the previous section, their pictorial representations will differ from those used for the more traditional approaches.

Cognitive Approaches

The increasing concern with cognition over the last 25 years has been welcomed by many as a revolution, or, at the least, as a long-overdue corrective to the "straitjacket" of behaviorism. Research has exploded on the processing, categorizing, and remembering of stimuli (e.g., Dickinson, 1980; Gallistel, 1990; Pearce, 1987; Roitblat, 1987). However, some researchers have damned the cognitive approach as a return to the unclear thinking and untestable mentalistic mediational concepts discarded at the beginning of this century.

A comparison of Figure 5 with the approaches of the behaviorists and Skinner (Figures 3 and 4) suggests support for aspects of both views. The additional complexity appears to be considerable compared to the models of the early behaviorists and Skinner, although

the model is quite similar to those of the neobehaviorists. The emphasis on processing of stimuli and the distinction between long-term (reference) memory and short-term (working) memory represent additions not clearly dealt with in neobehaviorism. But the sometimes glib discussions of these additions and the ambiguous role of consciousness also recall some of the problematic speculations of the introspectionists.

For our purposes, the useful aspect of the "cognitive revolution" is the acknowledgment and integration of research trends that have begun to fill in the causal path from consequence to response. Concepts such as affordances from perception (Gibson, 1979), stimulus filtering from ethology and neurophysiology (e.g., Leonard & McNaughton, 1990), multiple stimulus interaction from human performance and modern associative theory (e.g., Rescorla, 1988), and complex memory processing from cognitive science and neuroscience (e.g., Olton, 1978) have provided empirical support for the importance of considering stimulus processing and initial conditions in learning.

A renewal of interest in comparative cognition has produced evidence of unexpected complexity in the consequence-response sequence of many species (Wasserman, 1993). Chimpanzees use human sign language (Gardner, Gardner, & Van Cantfort, 1989), starlings mimic and rearrange human sounds and music (West & King, 1990), and rats and gray parrots can count (Davis & Perusse, 1988; Pepperberg, 1990). For the present purpose, the most interesting cases may be those in which processing is related to the ecology (initial conditions) of the species, as in the work of Cheney and Seyfarth (1990) on communication in vervet monkeys and Real (1991) on choice behavior and the evolution of "cognitive architecture" in bumblebees.

As to the issue of the loose use of mediational cognitive terms to explain behavior, it is certainly harmful when any concept is used primarily to construct explanations after the fact without adequate ties to the manipulation of independent variables or clear measurement. However, this problem is not confined to cognitive approaches. In the associationist/behaviorist tradition, concepts such as frustration and superstitious reinforcement sometimes have been invoked as after-the-fact explanations in

INFORMATION PROCESSING

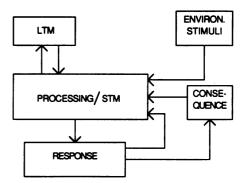


Fig. 5. The cognitive or information-processing model resembles the neobehaviorist model in positing increased stimulus inputs affecting reinforcement, including representations of responses, consequences, and the context. The cognitive approach adds to the neobehaviorist model a much greater concern with the nature of stimulus processing and the distinction between long- and short-term memory (LTM and STM).

both experimental and nonexperimental circumstances. For example, Skinner's (1948) invocation of adventitious reinforcement to explain "superstitious" behavior in pigeons was not anchored in experimental manipulations or the careful measurement of dependent variables. It appears to have been based on the relatively loose use of the mediational model that response increases are determined by contingent reinforcers (Timberlake & Lucas, 1985).

A remaining difficulty with the cognitive approach is that it is incomplete. As can be seen in Figure 5, the cognitive approach either ignores or downplays factors that can have critical effects in reinforcement situations. In many cases the cognitive approach is simply a complex version of the simple causal reinforcement model that still pays little attention to system issues of regulation, initial conditions, or the functions of responding. More attention to cognitive variables is part of the answer, but is not the whole solution.

Regulatory Approaches

Regulatory approaches manipulate traditional reinforcement variables, such as amount or proximity of reward, but predict the effects on responding from regulatory rather than associative or cognitive assumptions (e.g., Collier, 1983). The regulatory approach combines the notion of regulation from the domain of

biology with the idea of control processes from engineering and research on motor systems. Most importantly, the regulatory approach is explicitly a system view rather than a simple causal model (see Powers, 1973, 1989; Staddon, 1979). Reinforced responding is attributed to adjustments of the system of regulatory processes underlying free responding to the schedule-imposed constraints on response topography, timing, and amount.

A regulatory system approach not only increases the complexity of the reinforcement situation by introducing and requiring assessment of multiple regulated processes and balance points, but also considerably alters previous views of the response-consequence relation. In the traditional reinforcement view, the response-consequence relation is an independent causal variable, a response contingency imposed by the experimenter. The regulatory approach views the imposed contingency relation as a constraint on the causal variables underlying free responding. The obtained response-consequence relation is thus a dependent variable, the result rather than the cause of the adjustment of the organism to the imposed schedule.

By way of illustration, the experimenter can establish a specific schedule, such as requiring three key pecks to produce 3 s of hopper operation. But how often the animal completes this sequence and the actual contiguity, rate, and efficiency of key pecking and eating are all under the animal's control. Ultimately, the behavior of the organism under a schedule represents an adjustment in terms both of the response-consequence relation and the consequence-response relation. There is one independent variable—the elements of the putative feedback function designated by the experimenter—but many dependent variables, including the actual feedback function that results from, rather than causes, the organism's adjustment.

In most behavioral work, the regulatory tendencies of a system are inferred from the reliable response characteristics of relatively unconstrained (free baseline) behavior (Staddon, 1979; Timberlake, 1984). These equilibria or "set points" are behavioral, not physiological (although they may reflect internal processes such as metabolism or coordination of output). They are also characteristic of the environmental and organismic circumstances in which

they are assessed. Once estimates of such behavioral/circumstance set points are established, constraints can be placed on the system and the results referenced to the previous operation of the system. Any tendency of the system to maintain baseline characteristics under constraint provides critical evidence about regulatory processes underlying baseline behavior.

This strategy of assessing initial or "ideal" functioning prior to imposing constraint is used in a variety of other fields, including the study of motor systems (Kelso, 1982) and the economics and optimality of behavior (Belovsky, 1978; Schoener, 1971). For example, in motor research, the unconstrained operation of two motor oscillatory components may be measured prior to constraining or linking the two, with a view toward predicting their interaction. In optimal foraging research, set points of responding may be inferred from calculations of the minimal net energy required to maintain a particular "life-style" (Schoener, 1971; Stephens & Krebs, 1986). In the study of reinforcement, the paired baseline measurement of both instrumental and contingent responding allows the prediction of the circumstances of reinforcement with an accuracy not previously achieved.

Premack (1965) initially developed the paired (free) baseline as a technique to establish the relative reinforcement values of a set of responses by measuring their probabilities. Premack's intuition that any higher probability response would reinforce any lower probability response was an ambiguous appeal to both strengthening and regulatory ideas. What an unabashedly regulatory view like response deprivation (Timberlake & Allison, 1974) added was the explicit assumption that baseline probabilities reflected a balance point for the regulatory processes underlying each response in the baseline circumstances. Thus, the baseline level of a response is relevant to the prediction of reinforcement only to the extent that it is challenged by a schedule. Imposing a typical schedule relating, say, wheel running to eating challenges the baseline levels by linking the regulation of wheel running with the regulation of eating in a manner that conflicts with the baseline. The result is coregulation of the two responses with respect to their respective baseline set points. Typically, the less constrained response is driven above its base-

BEHAVIOR REGULATION

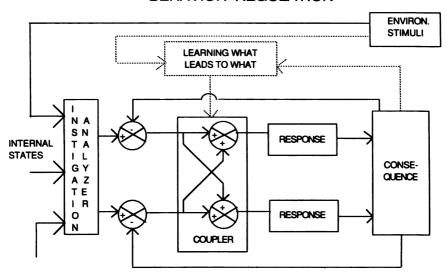


Fig. 6. The regulatory model includes separate feedback circuits for the instrumental and the contingent (reward) responses. Each feedback loop serves to regulate responding around its own level of motivation present in a situation (as input from the instigation analyzer). In general, stable levels of instigation produce stable baselines of responding. When an operant contingency is imposed (a schedule-based linkage between instrumental and contingent responding), the error signal from the initial comparator of each response is combined (cross-coupled) with the error signal of the other response to determine actual response output. The result is a system in which responding represents a compromise between the deviations from the set-points of the two responses linked by the schedule. As indicated by the dotted lines, stable responding, rather than learning, is emphasized.

line by the regulatory tendencies underlying the more constrained response (Hanson & Timberlake, 1983; Staddon, 1979; Timberlake, 1984).

Figure 6 illustrates how such a system view relates to the traditional reinforcement model. An obvious addition is the existence of two regulatory circuits instead of one, one loop for the contingent response (reinforcer-related response) and one for the instrumental (operant) response. A picture of an unconstrained baseline would simply show two regulatory circuits, the output of each driven by deviations from its own set point. Figure 6 shows that a contingency schedule couples the two regulatory circuits such that responding in each case is driven by the combination of the deviations from its own set point and the deviations from the other set point. The resultant coregulation of responding produces a balance point of responding differing from the baseline of either responses, a compromise of deviations (Hanson & Timberlake, 1983).

A primary difference from the traditional view is that the regulatory approach typically has few explicit ties to associationism or stimulus presentation. Some aspects of this are intentional. Schedule variables and stimulus manipulations commonly viewed as determinants of associative strength, such as contiguity, frequency, and amount or reliability of reward, are readily seen as constraints on free responding. Minimal assumptions about learned relations have been made. For example, Timberlake and Allison (1974) assumed only that the organism could learn "what leads to what." The remainder of responding was determined by adaptation to constraints on the expression of regulatory processes coupled with response selection comparators that promoted survival (Timberlake, 1984; Timberlake & Peden, 1987). Research in foraging and skill learning also leans toward viewing associative variables as constraints on or facilitators of regulation, instead of as associational causes of behavior.

Differences between a regulatory view of reinforcement and the traditional account may be easiest to convey using an analogy. Assume that a flowing river represents the baseline behavior of the animal, and a stick inserted in the water is the schedule. If the stick is held by someone standing on the bank, the result

will be a ripple (upsurge) of water climbing the upstream part of the stick. Although this fits a simple causal model relating the independent variable of inserting the stick to the upsurge of water, in reality the stream and stick make up a causal system. The key to the upsurge is neither the insertion of the stick nor the flowing of the river, but the relative movement of the stick and the river. If the person holding the stick in the river walked downstream at the precise rate the river was flowing, no upsurge would occur. In contrast, if the person walked downstream at a rate faster than the river was flowing, an upsurge would occur on the downstream instead of the upstream side of the stick.

In a not dissimilar way, schedules can produce increases, no effect, or decreases in the probability of a particular response. If the relative rate of responding imposed by the schedule (the stick) is less than the relative response rate in baseline (the river), an increase in the instrumental response will occur. If the relative response rates are the same, there will be no effect, and if the relative response rate imposed by the schedule is higher than in baseline, the instrumental response will decrease.

Without question, there are points for further analysis and development in the regulatory approach to reinforcement. The relative lack of concern with association and the analysis of stimulus control makes contact with traditional reinforcement notions more difficult. The notion of free baseline could profit from further development. For example, responding in free baseline does not represent a set point or an optimum so much as a settling point or, potentially, an "attractor," the value of which is affected by the stimulus circumstances. Baseline responding represents a balance or compromise among the causal forces operating in the situation; thus, responding will vary with the circumstances and the organismic state. Further, baseline responding for any particular response may not be optimal, either because competing processes prevent the optimum for a particular response from being reached or because mechanisms that have evolved under conditions of scarcity push responding too high in the absence of restrictions that were characteristic of the selection environment. For example, ingestion of unrestricted sucrose may not produce optimal behavior because the mechanisms driving intake evolved under conditions of scarcity to guide the animal toward readily assimilable calories.

Also, the notion that only total responding or overall foraging efficiency is regulated is too simple. There appear to be hierarchies and patterns of regulation ranging from local organization of responding through circadian and circannual rhythms. Some reliable patterns of responding appear regulated, and some do not. For example, Gawley, Timberlake, and Lucas (1986, 1987) showed that the disruption of some patterns of responding resulted in compensatory behaviors, and some did not. Integration of information about regulation and daily foraging activity patterns appears to be important at this point. Further, the conditions promoting baseline stability and change have received little attention.

A basic advantage of the regulatory approach is that it calls attention to variables that have been underrepresented in traditional reinforcement theory. Like the study of cognition, the study of behavioral regulation shifts the focus of attention to a different set of questions. For example, how is responding allocated and controlled across a variety of alternatives? What are the time periods over which animals respond to relative deficits and excesses, and with respect to what set points (Timberlake, Gawley, & Lucas, 1987)? The questions lean toward how animals function given a relaxation of the typical laboratory restrictions in the direction of more real-world settings (Collier, 1983; Timberlake & Lucas, 1991).

Ecological Approaches

The initial conditions and operating characteristics of an organism have to do with what evolutionary and individual history has provided in the way of structure and processes prior to the experimental manipulations of interest (Tinbergen, 1951). If we take seriously the notion that learning evolved as it produced a better fit with the environment, we must conclude that (a) learning evolved within the context of an already-functioning organism located in a particular ecology; (b) animals should come to any learning situation equipped with stimulus sensitivities, response components, and motivational states that should facilitate forms of learning appropriate to that ecology; and (c) what, how, and why something is learned will be a function of the fit of the initial conditions of the organism with the current environment. I will consider briefly two ecological approaches, constraints on learning and behavior systems.

Constraints on learning. The concept of constraints on learning was introduced in the early 1970s to increase the concern of reinforcement theory for initial conditions and more specialized types of learning. Beginning with concepts such as preparatory and consummatory motivational reactions (Konorski, 1967), adaptive specialization (Rozin & Kalat, 1971), learned release (Woodruff & Williams, 1976), speciesspecific defense reactions (Bolles, 1970), and the prefiguring hypothesis (Hollis, 1982), researchers have offered data and concepts that require the addition of initial conditions to the notions of traditional reinforcement theory. Much of the autoshaping and superstition literature showed clear indications of species, gender, and age-typical effects on topography (e.g., Timberlake & Lucas, 1989; Wasserman, 1973). Similar variables influence operant responding (e.g., Timberlake & Washburne, 1989).

Discoveries in this area also questioned the ability of the experimenter to establish the response-consequence relations as a simple causal sequence depending on contiguity. The prototypical work by Garcia and his many coworkers on long-delay taste aversion learning showed that poison consequences following a response by many hours could exert marked effects on the future intake of recent novel tastes (e.g., Garcia & Koelling, 1966). On a more modest time scale, Lattal and Gleeson (1990) showed that pigeons can learn to peck a key for food even if there is always a minimal delay of 30 s between pecking and food. An account of these results appears to require greater specification of the pathway from both the response to the consequence and the consequence back to subsequent responses.

Although constraints research pointed to several important and rather unexpected shortcomings of the simple causal approach to reinforcement, it appears to have had little permanent effect on the conceptual analysis of reinforcement. Like criticisms of a popular politician, constraints critiques have slowly sloughed off, leaving an increased general awareness of ecological factors but little change in the basic reinforcement approach. One rea-

son for the failure of such critiques to stick is that they were couched in terms of the structural elements of the simple causal reinforcement model (see Figure 3). Constraints were represented as variations in the strength of connections among stimuli, responses, and reinforcers rather than in terms of a more specific statement of how the organism functioned. From a systems view, constraints represent adaptations rather than limitations (Rozin & Schull, 1988). Predicting the conditions of their occurrence is a key to understanding them.

Behavior systems. A relatively general and comprehensive alternative to the constraints analysis of ecological variables was offered by Timberlake and Lucas (1989) in a behavior systems approach to learning (for similar approaches see Davey, 1989; Fanselow & Lester, 1988; Hogan, 1989; Timberlake, 1983a, 1983b, 1990). Timberlake and Lucas (1989) argued that learning evolved initially to support those experience-based alterations of already-functioning systems that allowed closer tracking of survival-related aspects of the environment. Thus, learning occurs and can be effectively studied within the context of a functional system.

Figure 7 represents the portion of a rat's feeding system that concerns predation (as opposed to browsing). The general "architecture" of this system owes much to classical ethology (e.g., Baerends & Drent, 1970; Tinbergen, 1951). The specifics of the perceptual motor modules and the subsystem shown in Figure 7 are grounded in the work of many independent investigators (Calhoun, 1962; Galef, 1990; Steininger, 1950; Telle, 1966) as well as in the observations and research of myself and my collaborators. Similar systems have been proposed by Davey (1989), Fanselow and Lester (1988), and Hogan (1989).

The system level of organization (not shown in Figure 7) refers to the tendency for behavior and stimulus processing to be organized around important functions, such as feeding or reproduction. Subsystems refer to combinations of stimulus sensitivities, response components, and motivational states that constitute strategies for adaptive functioning. Modes are motivational substates related to the sequential and temporal organization of behavior ranging from general search patterns to consummatory responses.

For example, a predatory feeding sequence

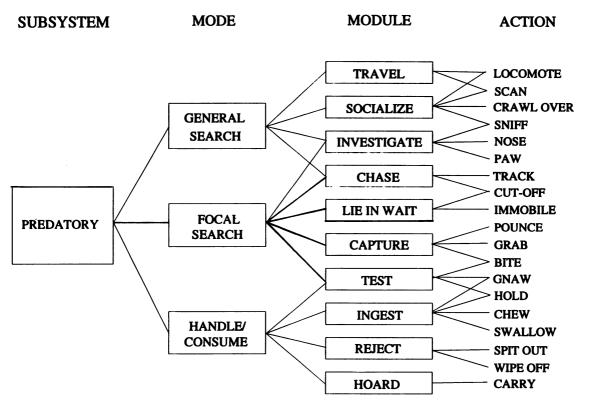


Fig. 7. The structure of a behavior system includes four levels: system, subsystem, motivational mode, and perceptual-motor modules. This figure illustrates the modes and modules of the predatory subsystem in the feeding system of the rat. Response-learning effects depend upon what search modes are conditioned and the modules best supported by the stimulus environment and the search modes.

in the rat typically begins with responding related to a general search mode, characterized by attention to novelty and search for cues that predict the location or timing of food. When cues occur that better predict food, the behavior of the animal reflects a focal search mode in which behavior is more focused and related to the immediate procurement of food. When food appears, the animal enters a handling or consuming mode. As the certainty of food drops following eating, the animal first reenters the focal search mode in the form of area-restricted search. In the absence of additional food, the rat returns to responding typical of a general search mode and finally switches to behavior typical of another system or quiescence. The lowest level of organization, perceptual motor modules, refers to probabilistic linkages between particular classes of stimulus sensitivities and components of responding that become integrated in terms of the stimulus control and action patterns of learned performance.

To researchers accustomed to the simple causal model of reinforcement, the behavior system shown in Figure 7 may appear unnecessarily complex. Part of the complexity is present because the standard models and diagrams of reinforcement have been greatly oversimplified to emphasize a simple causal link between the experimenter's manipulations and the effects on responding. This diagram attempts to include assumptions and information that typically are embedded in apparatus and procedures. But a more important reason for the diagram's complexity is that it represents (rather incompletely) a dynamic system of behavior, not just a simple causal model of reinforcement.

A behavior system is presumed to provide the preorganized materials for learning; it is the substrate that is integrated, linked, and differentiated under reinforcement procedures. Learning is assumed to occur at many points in a behavior system, in varied forms,

and as a function of conditions ranging from simple stimulus exposure to explicit response contingencies. For example, learning can involve the entrainment of motivational states to stimuli, the alteration and recombination of motor programs, the differentiation and combination of stimulus classes, and the integration and sequential combination of motor programs and stimulus classes. In many cases, learning effects follow the rules worked out in traditional studies of operant and Pavlovian conditioning, but there is no a priori commitment to force learning into these procedures. After all, learning did not evolve in terms of these paradigms but in terms of a functioning organism.

Although the complexity of a behavior system may appear to make it a better candidate for after-the-fact explanation than for a priori prediction, once a system is constructed from observations and previous experiments it is actually quite a powerful prediction device. Figure 7 is essentially a visual representation of a group of interrelated assumptions and hypotheses that can readily be put into words (see Timberlake, 1983b). For example, the diagram assumes that there are both general and specific motivational states (systems and subsystems vs. modes), that the more specific states (modes) show a sequential-temporal order with respect to the delivery of food, and that specific stimulus sensitivities and response components are grouped and related to particular modes. These assumptions allow predictions ranging from the effectiveness of particular stimuli in controlling behavior to the topography of behavior as a function of the type of predictive stimulus, the type of reward, and the interval between the predictive stimulus and the reward.

Timberlake and Lucas (1989) and Timberlake (1990) reviewed many examples of the use of behavior systems to predict learning as a function of the type and timing of the predictive stimulus. For example, social stimuli and moving stimuli should control, respectively, social and predatory behaviors in rats; brief predictive stimuli should control more focused behaviors, whereas longer stimuli control more general search. Predictions of species differences in reaction to types of predictive stimulus are often particularly clear. For example, presentation of food following presentation of a conspecific in rats should produce

social approach and contact, whereas in a hamster it should produce no effect or avoidance (Timberlake, 1983b). Based on their feeding ecology, different rodent species were predicted to react differently to contingencies involving moving stimuli (Timberlake & Washburne, 1989).

If after-the-fact accounts are a goal, the simple causal model of reinforcement is potentially more flexible than the behavior systems approach. To the extent that reinforcement is assumed to underlie increases in any characteristic of responding that reliably precedes reward, the simple reinforcement model can account for any outcome. Further, the simple causal approach also seems to be less flexible in incorporating improvements based on previous outcomes. The specifics of topography, timing, and stimulus sensitivity have little bearing on the simple causal model. In contrast, the direct ties to particular responses and stimuli allow the specifics of a behavior system to be improved conceptually by experimental results, an improvement that can then be used to improve subsequent predictions (see, e.g., the changes between the feeding systems shown in Timberlake, 1983b, and Timberlake & Lucas, 1989).

BEHAVIOR SYSTEMS AND REINFORCEMENT: REGULATION, ASSOCIATION, COGNITION, AND ECOLOGY

Given the simplified system framework with which we began, it has been relatively easy to see the different emphases and strengths of cognitive, regulatory, and ecological approaches to reinforcement. An intriguing possibility is that the combination of these approaches would make contact with a wider range of learning phenomena than any one alone. I suspect this proposal would meet with approval from many learning researchers who would assume that the traditional reinforcement account would serve as the framework for the resultant integration. I think, however, that this is not the most reasonable or heuristic strategy. These approaches have developed largely in parallel for over 20 years, with only slight evidence of overlap.

I believe a better alternative is to attempt to integrate regulatory, cognitive, and traditional associative views within a behavior systems

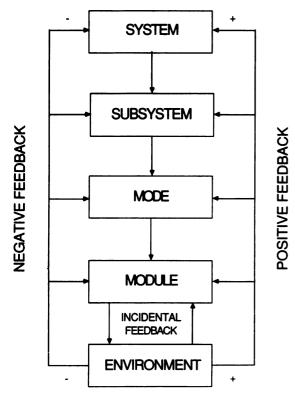


Fig. 8. A regulatory-behavior system model clarifies the relation between regulation and the hierarchical context of a behavior system. Regulatory feedback occurs at all levels of the system, not just at the level of overt responding shown in Figure 6. Positive feedback (instigation) also arises from activation at each level. Incidental feedback refers to the local adjustments of the organism that increase the fit of environment and responding.

approach. A behavior system provides a broader and more inclusive framework for study by emphasizing that learning occurs within an evolved, functional context. Regulatory and cognitive approaches are required in the analysis of any functional system, and the experimental paradigms of classic reinforcement theory provide a means to clarify and test the attributes of a behavior system. Further, because it is explicitly concerned with the form, function, and initial conditions of behavior, the behavior systems approach appears to be more readily integrated with knowledge about physiology, neurophysiology, and development. Below, I offer only the briefest of sketches of some advantages and possibilities of integrating these disparate approaches to reinforcement within a behavior systems context.

Regulation and Behavior Systems

Figure 8 provides a tentative illustration of how behavior regulation might be put together with a behavior systems approach to produce a hierarchical regulatory system. This figure abstracts the hierarchical levels of motivation from Figure 7 (system, subsystem, mode, and module) and shows the higher levels acting on the lower levels. In addition, Figure 8 shows three types of feedback from lower to higher levels. Negative feedback refers to the dissipative effects of behavior or the activation of a lower state on the activation of a higher state. Positive feedback refers to the excitatory or inertial effects of behavior or the activation of a lower state on the activation of a higher state. Incidental feedback is a term from the motor performance literature that refers to the immediate interaction (the local fit) of responding with the support and constraints of the environment (e.g., Bingham, 1988). Exactly how a particular system functions will depend on evolution and current circumstances.

A key question in the exploration of a regulatory system is what characteristics of the system are defended under environmental constraint. For example, Hogan and Roper (1978) reviewed considerable literature showing similarities and differences among commodities in the response characteristics preserved under schedule constraint (see also McFarland, 1973). Collier (e.g., 1983) has extensively documented the differences in requiring lever pressing for access to meals in rats as opposed to requiring lever pressing for access to individual bites. Rats adjust to the former by decreasing the frequency of meals and increasing the size. Rats adjust to the latter primarily by lever pressing more rapidly within a meal (see also Lucas & Timberlake, 1988).

A more complete behavior systems analysis of such regulatory phenomena will relate the form of the access requirement to appetitive strings leading to the constrained response under more naturally occurring circumstances. The importance of such appetitive strings can be seen in research by Gawley (1986) and Timberlake, Gawley, and Lucas (unpublished data) in which animals were required to wheel run for access to water in one case and food in another. Although running increased to maintain a reduced amount of eating and drinking in both cases, running in the case of

eating counted against (decreased) the noninstrumental running typical of the situation. In the case of drinking, instrumental running did not count against noninstrumental running, which remained at its baseline rate.

More complex examples of the importance of system variables in regulation also exist. Galef (1990) has demonstrated nicely how information about food sources is disseminated within the rat colony, giving precise social context, constraint, and repertoire to the expression of regulatory tendencies. Hogan (1984, 1989) has provided a careful analysis of how the feeding system in jungle fowl comes together developmentally, eventually to regulate in an adult-like fashion. Hollis (1990), in work with cichlid fish, has shown that preparatory responses to predictive cues can have significant advantages in successful territorial defense.

A final example of important system/regulation issues is the time horizon over which an organism's current behavior is modified to compensate for an increase or decrease in the availability of an important commodity. Considerable data show that an animal's behavior anticipates reliable seasonal decreases in access to food and warmth over a period of months. On a shorter time scale, however, abilities appear to be more limited. For example, Lucas, Timberlake, and Gawley (1989) showed that animals failed to increase premeal drinking in anticipation of the predictable absence of postmeal access to water. Timberlake, Gawley, and Lucas (1987, 1988) showed that rats did decrease current lever pressing in anticipation of an increase in food availability, but this decrease occurred primarily within the range of 8 to 16 min. Flaherty and Rowan (1986) and Lucas, Gawley, and Timberlake (1988) showed similar effects in a different paradigm. However, Lucas, Timberlake, Gawley, and Drew (1990) showed that the nature of the commodity (e.g., sucrose vs. Nutrasweet® or milk) can be a critical determinant of the time period of anticipation.

In short, the levels of regulation, the characteristics regulated, and the time horizons of regulation appear to depend on the organism's ecology, the mechanisms of assimilation of the commodity, and the type and amount of constraint. Such complexity may seem forbidding to researchers interested in general statements

cutting across systems and species. However, analyses of this complexity are critical to the understanding and application of reinforcement.

Associative Approaches and Behavior Systems

A major and still unresolved issue within associative theory has been to establish the unique circumstances that produce reinforcement. Classical theorists such as Hull (1952), Guthrie (1959), and Tolman (1932) proposed partially irreconcilable general mechanisms (e.g., drive reduction, contiguity of stimulus and response, and cognitive maps). Recent cognitive researchers have focused on a more complex quality, that of the surprisingness of stimulus-stimulus pairings. The regulatory approach argues that no single unique causal mechanism underlies reinforcement; instead, there are a set of circumstances that involve constraint on the expression of one or more motivational states. The behavior systems approach argues an even more complex view: The circumstances of reinforcement relate to environment-organism fitting processes that evolved to serve specific functions related to gene survival. Taken together, these views argue that there is no single mechanism for reinforcement, at least not at any behaviorally significant level. To oversimplify the point, Tolman, Guthrie, and Hull may all have been partly right but overly general and incomplete in their theoretical statements about the circumstances of reinforcement.

A more recent but related conflict has pitted the laboratory study of learning, which emphasizes arbitrary elements, artificial environments, and general laws, against ecological approaches such as behavior systems, which emphasize functional elements, evolutionary environments, and adaptive specializations. Jenkins (1979; personal communication) has suggested this split may be irreconcilable. I believe that again there may be less distance between approaches than might be thought.

First, laboratory researchers inevitably incorporate aspects of ecological and regulatory approaches in their tuning of the apparatus and procedures to the behavior of the organism. In other words, ecological concepts are used in practice but are omitted from theories. The importance of ecological variables is most obvious in the case of problematic phenomena, such as misbehavior, adjunctive behavior, superstitious behavior, and constraints on learning. These effects are readily interpreted and predicted within a behavior system that includes stimulus filtering, response components, and motivational states (Timberlake, 1990; Timberlake & Lucas, 1989). Specifically, animals in experiments using food as a reward draw on natural foraging sequences in their behavior. If these sequences are compatible with the imposed contingencies, responding is well behaved. If the natural sequences are incompatible with the imposed contingencies, misbehavior results.

Second, the integration of associative theory with a systems approach can facilitate the analysis of learning in functional contexts. Dropping the expectation that learning must occur only in terms of operant or Pavlovian procedures may facilitate the analysis of how learning actually occurs. For example, sharpening of stimulus control or integration of stimuli in the control of motor movements may occur by simple exposure in some cases and require contiguity with rewards in others. It is appropriate to analyze these results, not force them into a particular conception. Also, researchers such as Davey (1989), Holland (1984), Hollis (1990), Sevenster (1973), Shettleworth (1975), and Timberlake (1983a, 1983b, 1990) have shown that laboratory paradigms and concepts can be powerful tools in exploring the nature of the system structure related to learning.

Finally, if the behavior systems approach truly provides a framework for laboratory learning, then it also must account for the widespread success of learning arbitrary tasks in artificial environments. The explanation is straightforward, though not simple. Learning is not arbitrary. Animals did not evolve in arbitrary environments; therefore, there are no stimulus filters, response components, and motivational states designed to deal with arbitrary environments. When an animal encounters an arbitrary (from the experimenter's view) task, it engages it with the nonarbitrary (evolved and developed) structure that most closely fits.

Some system structures may be specific to a particular functional task, whereas others may be more general in function. There should be generalized qualities of most environments that encourage the borrowing or convergent evolution of similar structures, although limits on this generality should exist. Thus, it would not

be surprising to find "causality detectors" (one or more mechanisms for indexing contingencies between stimuli) in most systems and species, although it would be surprising if they were identical in operation. Similarly, it would be expected that kinds of behavior associated with general search would be more resistant to extinction than those associated with focal search and handling.

In short, placing associative learning within a behavior systems framework does not prejudge that there are no generalizable laws; it simply grounds such questions in evolution and functionality. The result is a concern with both diversity and generality, rather than one or the other. The approach also generates potentially disprovable general and specific hypotheses and encourages the treatment of associative paradigms as tools to investigate how learning is embedded in the structures and processes that underlie behavior. From a behavior systems view, the procedures of Pavlovian and operant conditioning constrain the same underlying system, although in somewhat different ways.

Cognition: Stimulus Processing and Memory Within Systems

A complete account of learning in any ecological setting must consider in some form the issues of stimulus filtering, processing, storage, and retrieval. In terms of the development of stimulus processing in the context of a particular system of behavior, Hailman's (1967) work on the ontogeny of directed pecking in gulls is a very nice representation of how a behavior systems approach can be joined with cognitive and associational accounts to produce an inspiring initial attempt at understanding development. Other instances of systems-specific filtering and learning have been reported by Baerends and Drent (1970, section 4) in the treatment of eggs by nesting herring gulls, by Losey (1982) concerning the treatment by damselfish of interspecific intruders, and by Hogan (1989) in the development of feeding behavior in chicks.

A great amount of work has been done on memory for food caches in some passerine birds. After considerable field work demonstrating that Clark's nutcrackers can remember their prior cache sites for over a year, Balda and Kamil (1989) demonstrated that expected differences between nutcrackers and similar species were obtained in more artificial conditions as well. It would be of some interest to know

if similar abilities can be shown with water as a reward. Similar laboratory comparisons of memory between species differing in extent of caching have also been reported by Krebs, Healy, and Shettleworth (1990). Worth noting is that tests of performance on common laboratory tasks often show smaller differences among species than tests in more natural settings (e.g., Olson, 1991). This should not be surprising, given that common laboratory circumstances may not be well tuned to the operation of a system in a particular species.

In a provocative paper, Sherry and Schacter (1987) proposed an evolutionary approach to the question of multiple forms of memory. Beginning with data on both nonhumans and humans indicating the existence of more than one memory type, they argued that different types of memory should have evolved when the functions of and restrictions on memory processes were incompatible with other forms of memory. For example, memory for songs in most passerine birds requires selectivity for species song, long-term retention without modification, and some restriction on the period of acquisition. In contrast, memory for recovering cached food has no obvious restriction on input, no restriction to particular times of year, and rapid forgetting once the food cache has been retrieved. Having one type of memory serve the other function would not be as effective.

A similar analysis might be made of Garcia's work on different defensive systems (e.g., Garcia & Garcia y Robertson, 1985). Garcia and his co-workers have pointed out the marked differences between the skin and gut defensive systems in terms of stimulus control, potentiation effects, and speed of learning. The skin defensive system (related to the somatic sensory neuropil and the striated muscle system) mediates the rapid learning of avoidance of most environmental cues including odor, but not taste, cues. The gut defensive system (related to the visceral sensory neuropil and the smooth muscles of the gastrointestinal tract) pays closest attention to novel and salient tastes rather than environmental cues, but can potentiate the avoidance of odors. It also is capable of easily bridging very long delays between cue and consequence.

Using the form of argument raised by Sherry and Schacter (1987) with respect to memory systems, one could argue that the existence of separate defense systems for skin and gut would be expected because of the incompatible de-

mands for operation in each case. Skin defense in general must track many environmental cues, especially rapid movement, but not necessarily taste. Gut defense should track taste alone unless there are highly reliable and frequently repeated environmental cues. Among alternative cues, odor would be expected to be high on the list. Context cues should be slow to acquire control and more rapid to extinguish (see Melcer & Timberlake, 1985).

An interesting side effect of behavior systems analysis in general, but especially the cognitive/sensory forms illustrated in these last two examples, is the rapid emergence of potential ties to physiology. Traditional causal reinforcement theories have long tried to make contact with physiological analyses, but the results have often been less than satisfactory. Despite the presumptive connectionism of most learning models, researchers have only recently begun to trace the circuitry involved in "simple" learning (e.g., Thompson, 1986). Placing learning within a functional context involving sensory filtering, motor components, and specificity of function appears to provide more opportunity for interaction with neurophysiological analyses and techniques (e.g., Kesner & Olton, 1990). Although not a panacea for resolving reinforcement issues, contact with a physiological level of analysis can identify mechanisms that help to clarify the nature and limitations of reinforcement effects at a more behavioral level.

CONCLUSIONS

American behaviorists translated the observations and speculations of British associationists into reinforcement theory, a powerful experimental approach to the learning of purposive behavior. According to the simple causal reinforcement model, learning is produced by the direct action of a reinforcer on the future strength of a response. Despite the splintering of the behaviorist approach over the last 30 years, there has been a tendency for researchers to hold to this simple causal approach. It is apparently straightforward to test, easily portable from one circumstance to another, and promotes fundamental agreement on the important issues, thereby evading time-consuming and unresolvable theoretical conflicts.

However, numerous examples of recent research show that the determinants of learning are more complex than is easily allowed for in a simple causal model (e.g., Timberlake & Lucas, 1989). As researchers more carefully analyze specific examples of learning, the reinforcement concept often becomes less, rather than more, useful in pinpointing important variables. Many research areas (e.g., concept learning, developmental psychology), after embracing a reinforcement approach for a time, have largely abandoned it as not comprehensive. Even within the traditional reinforcement approach, the critical importance of carefully tuning the apparatus and procedures to fit the phenomena to the simple causal model has been increasingly evident (e.g., Timberlake, 1990).

I believe the clarification and amplification of the phenomena of reinforcement begin with a systems approach that focuses explicitly on the way in which the organism fits with the environment. It is a functioning organism, after all, not a billiard ball rolling on a slate table (Zeiler, 1992). Isolating simple causal reinforcement effects to study them more carefully was an important step in developing a science of behavior, but we must now start to reassemble reinforcement and behavior. To begin with, a distinction must be made between the independent variable manipulated by the experimenter and the basis for the subsequent change in responding. At the least, it should be noted that the response-consequence relation specified by the experimenter is not what typically occurs. The animal adjusts both the consequence-response relation and the response-consequence relation to the environmental constraints. Thus, a simple experimental manipulation is complexly related to several output measures, and the simple causal paradigm is, to a surprising degree, always violated.

As to the use of tuning and motivational boundary conditions to maintain the simplicity of the reinforcement model, I believe our research would be better served by placing motivation and the results of tuning as variables in more complex models of learned behavior. Presumed boundary conditions should not be used to restrict research, but should be studied in their own right. For example, the boundary condition of constant session motivation in operant research is probably never met (e.g., McSweeney, 1992), but its invocation has inhibited working out the hierarchies of regulation underlying learned behavior (Timber-

lake & Peden, 1987). The boundary conditions imposed by the use of particular stimuli, responses, and environments should give us, if we can read them right, information about the evolution and ecology of the species we work with and hints about their relation to learning.

Also, boundary conditions that take the form of focusing on a particular "correct" conceptual paradigm can interfere markedly with the discovery and understanding of the phenomena. If Pavlov had adopted a strict boundary-condition approach to the study of salivation, he would have ignored anticipatory salivation because it did not fit the simple causal model of digestion. Salivation in advance of food in the mouth is clearly not a pure measure of the digestive reflex, and a more cautious scientist might well have worked to eliminate its occurrence.

Some researchers may fear that abandonment of the simple causal model of reinforcement will surrender scientific rigor and even admit mentalism or teleology as explanations of behavior. To me, the primary issue here is not mentalism versus mechanism or teleology versus selectionism, but whether our focus is on simple causal models or causal systems. A reinforcer treated as an isolated causal entity loses contact with the context and becomes a mediational concept subject to the same vagaries that confront the use of more mentalistic concepts. Antecedent conditions are left uncertain, and outcomes are simplified to fit the model. It becomes difficult to avoid reasoning backwards from effects to simple causes rather than forward from manipulations to a more complex characterization of the results.

If we are to continue to use the term and technology of reinforcement to good effect, three steps must be taken. First, we must forsake the simple strengthening model, using it only as a first approximation, a rule of thumb when there is not time or resources to do more. Because we can control behavior by presenting a response-contingent reinforcer does not mean that the reinforcer is an isolated causal variable, insulated from known details of the structure and processes of ongoing causal systems. Second, we should adopt a functional systems approach, broadening our concerns to include the study of cognitive, regulatory, and ecological determinants. The resultant approach may at first appear ungainly, a theoretical analogue of the odd-looking wildebeest, the African antelope apparently put together by a committee. But like the wildebeest, such a theory may well prove more successful in the long run than sleeker versions designed for one purpose alone. Third, the concept of reinforcement must be ruthlessly analyzed and dissected with the same enthusiasm with which Skinner (1950) took apart the necessity of learning theories, but without limiting ourselves to overly simple visions of causation that ignore the structure and processes involved in a causal system.

Paradoxically, the best strategy for recapturing the importance of reinforcement and continuing its analysis may be to decrease its apparent power by clarifying its complexity and relation to function (Timberlake, 1990; Timberlake & Lucas, 1989). Rather than serving as the simple, basic constructor of behavior, reinforcement is better viewed as a modifier of an already-functioning biological system. In such a system, learning can be viewed as the entrainment, coupling, integration, differentiation, and replication of hierarchical regulatory structures. The traditional variables of frequency and temporal and spatial contiguity are still important. But other variables, such as stimulus support, disequilibrium conditions, memory, stimulus processing and integration, and even selection environment and gene pool, are critical as well. These are all fundamental contributors to a causal system, not modifiers of the expression of a simple causal or selectionist process.

REFERENCES

- Baerends, G. P., & Drent, R. H. (1970). The herring gull and its eggs. *Behaviour*, 17 (Supplement), 1-416.
- Balda, R. P., & Kamil, A. C. (1989). A comparative study of cache recovery in three corvid species. *Animal Behaviour*, 38, 486-495.
- Baum, W. M. (1973). The correlation-based law of effect. Journal of the Experimental Analysis of Behavior, 20, 137-153.
- Belovsky, G. E. (1978). Dieet optimization in a generalist herbivore: The moose. *Theoretical Population Biology*, 14, 105-134.
- Bingham, G. P. (1988). Task-specific devices and the perceptual bottleneck. Human Movement Science, 7, 225-264.
- Bolles, R. C. (1970). Species-specific defense reactions and avoidance learning. *Psychological Review*, 77, 32-42
- Breland, K., & Breland, M. (1966). Animal behavior. New York: Macmillan.
- Brown, P. L., & Jenkins, H. M. (1968). Auto-shaping of the pigeon's key-peck. *Journal of the Experimental Analysis of Behavior*, 11, 1-8.

- Calhoun, J. B. (1962). The ecology and sociology of the Norway rat. Bethesda, MD: U.S. Department of Health, Education, and Welfare, Publication 1008.
- Catania, A. C., & Reynolds, G. S. (1968). A quantitative analysis of the responding maintained by interval schedules of reinforcement. Journal of the Experimental Analysis of Behavior, 11, 327-383.
- Cheney, D. L., & Seyfarth, R. M. (1990). How monkeys see the world: Inside the mind of another species. Chicago: University of Chicago Press.
- Collier, G. H. (1983). Life in a closed economy: The ecology of learning and motivation. In M. D. Zeiler & P. Harzem (Eds.), Advances in analysis of behaviour: Vol. 3. Biological factors in learning (pp. 223-274). Chichester, England: Wiley.
- Davey, G. (1989). Ecological learning theory. New York: Routledge.
- Davis, H., & Perusse, R. (1988). Numerical competence in animals: Definitional issues, current evidence, and a new research agenda. Behavioral and Brain Sciences, 11, 561-615.
- Dickinson, A. (1980). Contemporary animal learning theory. Cambridge: Cambridge University Press.
- Fanselow, M. S., & Lester, L. S. (1988). A functional behavioristic approach to aversively motivated behavior: Predatory imminence as a determinant of the topography of defensive behavior. In R. C. Bolles & M. D. Beecher (Eds.), Evolution and learning (pp. 185-212). Hillsdale, NJ: Erlbaum.
- Fantino, E., & Abarca, N. (1985). Choice, optimal foraging, and the delay-reduction hypothesis. *Behavioral* and *Brain Sciences*, 8, 315-330.
- Flaherty, C. F., & Rowan, G. A. (1986). Successive, simultaneous, and anticipatory contrast in the consumption of saccharin solutions. *Journal of Experimental Psychology: Animal Behavior Processes*, **12**, 381-393.
- Galef, B. G., Jr. (1990). An adaptionist perspective on social learning, social feeding, and social foraging in Norway rats. In D. A. Dewsbury (Ed.), Contemporary issues in comparative psychology (pp. 55-79). Sunderland, MA: Sinauer.
- Gallistel, C. R. (1990). The organization of learning. Cambridge, MA: MIT Press.
- Gannon, K. N., Smith, H. V., & Tierney, K. J. (1983). Effects of procurement cost on food consumption in rats. Physiology and Behavior, 31, 331-337.
- Garcia, J., & Garcia y Robertson, R. (1985). Evolution of learning mechanisms. In B. L. Hammonds (Ed.), Psychology and learning: The master lecture series (Vol. 4, pp. 187-243). Washington, DC: American Psychological Association.
- Garcia, J., & Koelling, R. A. (1966). Relation of cue to consequence in avoidance learning. Psychonomic Science, 4, 123-124.
- Gardner, R. A., & Gardner, B. T. (1988). Feedforward versus feedbackward: An ethological alternative to the law of effect. Behavioral and Brain Sciences, 11, 429-446.
- Gardner, R. A., Gardner, B. T., & Van Cantfort, T. E. (1989). Teaching sign language to chimpanzees. Albany, NY: State University of New York Press.
- Gawley, D. J. (1986). Local and molar mechanisms in behavior regulation. Unpublished doctoral dissertation, Indiana University, Bloomington.
- Gawley, D. J., Timberlake, W., & Lucas, G. A. (1986).

- Schedule constraint of average drink-burst length and the regulation of wheel running and drinking in rats. *Journal of Experimental Psychology: Animal Behavior Processes*, 12, 78-94.
- Gawley, D. J., Timberlake, W., & Lucas, G. A. (1987). System-specific differences in behavior regulation: Overrunning and under-drinking in molar non-depriving schedules. Journal of Experimental Psychology: Animal Behavior Processes, 13, 354-365.
- Gibson, J. J. (1979). The ecological approach to visual perception. Boston: Houghton Mifflin.
- Guthrie, E. R. (1959). Association by contiguity. In S. Koch (Ed.), Psychology: A study of a science: Vol. 2. General systematic formulations, learning, and special processes (pp. 158-195). New York: McGraw-Hill.
- Hailman, J. P. (1967). The ontogeny of an instinct. Behaviour Supplements, 15, 1-159.
- Hanson, S. J., & Timberlake, W. (1983). Regulation during challenge: A general model of learned performance under schedule constraint. *Psychological Review*, 90, 261-282.
- Herrnstein, R. J. (1970). On the law of effect. Journal of the Experimental Analysis of Behavior, 13, 243-266.
- Hogan, J. A. (1984). Pecking and feeding in chicks. Learning and Motivation, 15, 360-376.
- Hogan, J. A. (1989). Cause and function in the development of behavior systems. In E. M. Blass (Ed.), Handbook of behavioral and neurobiology (Vol. 9, pp. 63-106). New York: Plenum Press.
- Hogan, J. A., & Roper, T. J. (1978). A comparison of the properties of different reinforcers. In J. S. Rosenblatt, R. A. Hinde, C. Beer, & M. C. Busnel (Eds.), Advances in the study of behavior (Vol. 8, pp. 155-255). New York: Academic Press.
- Holland, P. C. (1984). Origins of Pavlovian conditioned behavior. In G. H. Bower (Ed.), The psychology of learning and motivation (Vol. 18, pp. 129-173). Englewood Cliffs, N.J.: Prentice-Hall.
- Hollis, K. L. (1982). Pavlovian conditioning of signal-centered action patterns and autonomic behavior: A biological analysis of function. In J. S. Rosenblatt, R. A. Hinde, C. Beer, & M. C. Busnel (Eds.), Advances in the study of behavior (pp. 1-64). New York: Academic Press.
- Hollis, K. L. (1990). The role of Pavlovian conditioning in territorial aggression and reproduction. In D. A. Dewsbury (Eds.), Contemporary issues in comparative psychology (pp. 197-219). Sunderland, MA: Sinauer.
- Hull, C. L. (1952). A behavior system. New Haven, CT: Yale University Press.
- Jenkins, H. M. (1979). Animal learning and behavior theory. In E. Hearst (Ed.), The first century of experimental psychology (pp. 177-228). Hillsdale, NJ: Erlbaum.
- Kelso, J. A. (1982). The process approach to understanding human motor behavior: An introduction. In J. A. Kelso (Ed.), Human motor behavior: An introduction (pp. 3-20). Hillsdale, NJ: Erlbaum.
- Kesner, R. P., & Olton, D. S. (Eds.). (1990). Neurobiology of comparative cognition. Hillsdale, NJ: Erlbaum.
- Killeen, P. R. (1988). The reflex reserve. Journal of the Experimental Analysis of Behavior, 50, 319-331.
- Kimble, G. A. (1961). Hilgard & Marquis' conditioning and learning (2nd ed.). New York: Appleton-Century-Crofts.
- Konorski, J. (1967). Integrative activity of the brain: An

- interdisciplinary approach. Chicago: University of Chicago Press.
- Krantz, D. H. (1972). Measurement structures and psychological laws. Science, 175, 1427-1435.
- Krebs, J. R., Healy, S. D., & Shettleworth, S. J. (1990). Spatial memory of Paridae: Comparison of a storing and a nonstoring species, the coal tit, *Parus ater*, and the great tit, *P. major. Animal Behavior*, 39, 1127-1137.
- Lattal, K. A., & Gleeson, S. (1990). Response acquisition with delayed reinforcement. Journal of Experimental Psychology: Animal Behavior Processes, 16, 27-39.
- Leonard, B., & McNaughton, B. L. (1990). Spatial representation in the rat: Conceptual, behavioral, and neurophysiological perspectives. In R. P. Keesner, & D. S. Olton (Eds.), Neurobiology of comparative cognition (pp. 363-422). Hillsdale, NJ: Erlbaum.
- Losey, G. S., Jr. (1982). Ecological cues and experience modify interspecific aggression by the damselfish, Stegastes fasciolatus. Behaviour, 81, 14-37.
- Lucas, G. A., Gawley, D. J., & Timberlake, W. (1988). Anticipatory contrast as a measure of time horizons in the rat: Some methodological determinants. *Animal Learning & Behavior*, 16, 377-382.
- Lucas, G. A., & Timberlake, W. (1988). Interpellet delay and meal patterns in the rat. Physiology & Behavior, 43, 259-264.
- Lucas, G. A., Timberlake, W., & Gawley, D. J. (1989). Learning and meal-associated drinking: Meal-related deficits produce adjustments in postprandial drinking. *Physiology & Behavior*, 46, 361-367.
- Lucas, G. A., Timberlake, W., Gawley, D. J., & Drew, J. (1990). Anticipation of future food: Suppression and facilitation of saccharin intake depending on the delay and type of future food. Journal of Experimental Psychology: Animal Behavior Processes, 16, 169-177.
- MacCorquodale, K., & Meehl, P. E. (1954). Edward
 C. Tolman. In W. K. Estes & W. S. Verplanck (Eds.),
 Modern learning theory: A critical analysis of five examples
 (pp. 177-266). New York: Appleton-Century-Crofts.
- McFarland, D. (1973). Stimulus relevance and homeostasis. In R. A. Hinde & J. Stevenson-Hinde (Eds.), Constraints on learning: Limitations and predispositions (pp. 141-156). London: Academic Press.
- McSweeney, F. K. (1992). Rate of reinforcement and session duration as determinants of within-session patterns of responding. Animal Learning & Behavior, 20, 160-169
- Melcer, T., & Timberlake, W. (1985). Poison avoidance and patch (location) selection in rats. *Animal Learning & Behavior*, **13**, 60-68.
- Michael, J. L. (1985). Behavior analysis: A radical perspective.
 In B. L. Hammonds (Ed.), Psychology and learning: The master lecture series (Vol. 4, pp. 95-121).
 Washington, DC: American Psychological Association.
- Michotte, A. (1946). La perception de la causalite. Louvain: Institut Superieur de Philosophie.
- Morgan, C. L. (1896). Habit and instinct. London: Arnold.
- Nevin, J. A., & Baum, W. M. (1980). Feedback functions for variable-interval reinforcement. *Journal of the Experimental Analysis of Behavior*, 34, 207-217.
- Olson, D. J. (1991). Species differences in spatial memory among Clark's nutcrackers, scrub jays, and pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, 17, 363-376.
- Olton, D. S. (1978). Characteristics of spatial memory.

- In S. H. Hulse, H. Fowler, & W. K. Honig (Eds.), Cognitive processes in animal behavior (pp. 341-373). Hillsdale, NJ: Erlbaum.
- Pavlov, I. P. (1927). Conditioned reflexes: An investigation of the physiological activity of the cerebral cortex. (G. V. Anrep, trans.). London: Oxford University Press.
- Pearce, J. M. (1987). An introduction to animal cognition. Hillsdsale, NJ: Erlbaum.
- Pepperberg, I. M. (1990). Some cognitive capacities of an African grey parrot (*Psittacus erithacus*). Advances in the Study of Behaviour, 19, 357-409.
- Powers, W. T. (1973). Behavior: The control of perception. Chicago: Aldine Publishing.
- Powers, W. T. (1989). Living control systems. Gravel Switch, KY: The Control Systems Group, Inc.
- Premack, D. (1965). Reinforcement theory. In D. Levine (Ed.), Nebraska Symposium on Motivation (Vol. 13, pp. 123-180). Lincoln: University of Nebraska Press.
- Rashotte, M. E., & Henderson, D. (1988). Coping with rising food costs in a closed economy: Feeding behavior and nocturnal hypothermia in pigeons. *Journal of the Experimental Analysis of Behavior*, 50, 441-456.
- Ray, R. D., & Delprato, D. J. (1989). Behavior systems analysis: Methodological strategies and tactics. Behavioral Science, 34, 81-127.
- Real, L. A. (1991). Animal choice behavior and the evolution of cognitive architecture. Science, 253, 980– 986
- Rescorla, R. A. (1988). Pavlovian conditioning: It's not what you think it is. *American Psychologist*, **43**, 151-160.
- Roitblat, H. L. (1987). Introduction to comparative cognition. New York: Freeman.
- Rozin, P., & Kalat, J. N. (1971). Specific hungers and poison avoidance as adaptive specializations of learning. *Psychological Review*, 78, 459-486.
 Rozin, P., & Schull, J. (1988). The adaptive-evolution-
- Rozin, P., & Schull, J. (1988). The adaptive-evolutionary point of view in experimental psychology. In R.
 C. Atkinson, R. J. Herrnstein, G. Lindzey, & R. D.
 Luce (Eds.), Stevens' handbook of experimental psychology (pp. 503-546). New York: Wiley.
- Schoener, T. W. (1971). Theory of feeding strategies. Annual Review of Ecology and Systematics, 2, 369-404.
- Sevenster, P. (1973). Incompatibility of response and reward. In R. A. Hinde & J. Stevenson-Hinde (Eds.), Constraints on learning: Limitations and predispositions (pp. 265-283). New York: Academic Press.
- Sherry, D. F., & Schacter, D. L. (1987). The evolution of multiple memory systems. *Psychological Review*, 94, 439-454.
- Shettleworth, S. J. (1975). Reinforcement and the organization of behavior in golden hamsters: Hunger, environment, and food reinforcement. Journal of Experimental Psychology: Animal Behavior Processes, 1, 56–87.
- Skinner, B. F. (1938). The behavior of organisms. New York: Appleton-Century.
- York: Appleton-Century.
 Skinner, B. F. (1948). "Superstition" in the pigeon.

 Journal of Experimental Psychology, 38, 168-172.
- Skinner, B. F. (1950). Are theories of learning necessary? Psychological Review, 57, 193-216.
- Skinner, B. F. (1953). Science and human behavior. New York: Macmillan.
- Skinner, B. F. (1966). The phylogeny and ontogeny of behavior. *Science*, **153**, 1205-1213.
- Skinner, B. F. (1981). Selection by consequences. Science, 213, 501-504.

- Skinner, B. F. (1989). The origins of cognitive thought. *American Psychologist*, **44**, 13-18.
- Staddon, J. E. R. (1979). Operant behavior as adaptation to constraint. *Journal of Experimental Psychology:* General, 108, 48-67.
- Staddon, J. E. R. (1980). Optimality analyses of operant behavior and their relation to optimal foraging. In J. E. R. Staddon (Ed.), Limits to action: The allocation of individual behavior (pp. 101-142). New York: Academic Press.
- Steininger, F. von (1950). Beitrage zur soziologie und sonstigen biologie der wanderatte, Zeitschrift fur Tierpsychologie, 7, 356-379.
- Stephens, D. W., & Krebs, J. R. (1986). Foraging theory. Princeton, N.J.: Princeton University Press.
- Telle, J. J. (1966). Beitrage zur kenntnis der verhaltensweise von ratten, vergleichend dargestellt bei, Rattus norvegicus und Rattus rattus. Zeitschrift fur Angewandts Zoologie, 53, 129-196.
- Thompson, R. F. (1986). The neurobiology of learning and memory. Science, 233, 941-947.
- Thorndike, E. L. (1898). Animal intelligence: An experimental study of the associative processes in animals. *Psychological Review Monograph Supplements*, 2 (4, Whole No. 8).
- Timberlake, W. (1983a). Appetitive structure and straight alley running. In R. Mellgren (Ed.), *Animal cognition and behavior* (pp. 163-222). Amsterdam: North Holland Press.
- Timberlake, W. (1983b). The functional organization of appetitive behavior: Behavior systems and learning. In M. D. Zeiler & P. Harzem (Eds.), Advances in the analysis of behavior: Vol. 3. Biological factors in learning (pp. 177-221). London: Wiley.
- Timberlake, W. (1984). Behavior regulation in learned performance: Some misapprehensions and disagreements. Journal of the Experimental Analysis of Behavior, 41, 355-375.
- Timberlake, W. (1988). The Behavior of Organisms: Purposive behavior as a type of reflex. Journal of the Experimental Analysis of Behavior, 50, 305-317.
- Timberlake, W. (1990). Natural learning in laboratory paradigms. In D. A. Dewsbury (Ed.), Contemporary issues in comparative psychology (pp. 31-54). Sunderland, MA: Sinauer.
- Timberlake, W., & Allison, J. (1974). Response deprivation: An empirical approach to instrumental performance. *Psychological Review*, **81**, 146-164.
- Timberlake, W., & Farmer-Dougan, V. A. (1991). Reinforcement in applied settings: Figuring out ahead of time what will work. *Psychological Bulletin*, 110, 379–391.
- Timberlake, W., Gawley, D. J., & Lucas, G. A. (1987). Time horizons in rats foraging for food in temporally separated patches. *Journal of Experimental Psychology:* Animal Behavior Processes, 13, 302-309.
- Timberlake, W., Gawley, D. J., & Lucas, G. A. (1988). Time horizons in rats: The effect of operant control of access to future food. *Journal of the Experimental Analysis of Behavior*, **50**, 405-417.
- Timberlake, W., & Lucas, G. A. (1985). The basis of superstitious behavior: Chance contingency, stimulus substitution, or appetitive behavior? *Journal of the Experimental Analysis of Behavior*, 44, 279-299.
- Timberlake, W., & Lucas, G. A. (1989). Behavior systems and learning: From misbehavior to general principles. In S. B. Klein & R. R. Mowrer (Eds.), Concording the Control of the Control

- temporary learning theories: Instrumental conditioning theory and the impact of biological constraints on learning (pp. 237-275). Hillsdale, NJ: Erlbaum.
- Timberlake, W., & Lucas, G. A. (1991). Periodic water, interwater interval, and adjunctive behavior in a 24-hour multi-response environment. *Animal Learning & Behavior*, 19, 369-380.
- Timberlake, W., & Peden, B. F. (1987). On the distinction between open and closed economies. *Journal of the Experimental Analysis of Behavior*, **48**, 35-60.
- Timberlake, W., & Washburne, D. L. (1989). Feeding ecology and laboratory predatory behavior toward live and artificial moving prey in seven rodent species. Animal Learning & Behavior, 17, 1-10.
- Tinbergen, N. (1951). The study of instinct. Oxford: Clarendon Press.
- Tolman, E. C. (1932). Purposive behavior in animals and men. New York: Century.
- Warren, H. C. (1921). A history of the association psychology. New York: Scribners.

- Wasserman, E. A. (1973). Pavlovian conditioning with heat reinforcement produces stimulus-directed pecking in chicks. *Science*, **181**, 875–877.
- Wasserman, E. A. (1993). Comparative cognition: Beginning the second century of the study of animal intelligence. *Psychological Bulletin*, 113, 211-228.
- West, M. J., & King, A. P. (1990). Mozart's starling. American Scientist, 78, 108-114.
- Woodruff, G., & Williams, D. R. (1976). The associative relation underlying autoshaping in the pigeon. *Journal of the Experimental Analysis of Behavior*, **26**, 1-13.
- Zeiler, M. D. (1992). On immediate function. Journal of the Experimental Analysis of Behavior, 57, 417-427.

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